

Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*

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ABSTRACT: Competition between corals and algae is an important process on coral reefs, especially during reef degradation, when abundant corals are often overgrown by benthic macroalgae. Despite the widespread assumption that macroalgae are able to out-compete corals for space, there have been very few experimental studies testing the nature of this interaction. This study compared the effects of a filamentous red alga, *Anotrichium tenue*, with those of mixed-species, filamentous algal turfs on massive *Porites* spp. corals on inshore reefs of the central Great Barrier Reef, Australia. We compared mortality of coral tissue in plots with *A. tenue* naturally present on live coral tissue, plots in which *A. tenue* was naturally present but experimentally removed, and plots where mixed algal turfs were naturally present but *A. tenue* was not. The results indicate that *A. tenue* killed coral tissue by active overgrowth. Removing the alga removed the effect. In contrast, general, mixed-species algal turfs did not cause any mortality of coral tissue. We suggest that 2 particular traits of *A. tenue* may facilitate its effects on the corals. First, unlike most filamentous turf species present, it was able to overgrow live coral tissue, perhaps due to allelochemical effects. Second, individual algal filaments trap relatively large amounts of mucus from the corals and of sediment, apparently increasing the damage to underlying coral tissue. Surveys indicated that *A. tenue* primarily affected massive *Porites* spp., that overgrowth effects were not site-specific, but that occurrence of infected corals was not widespread. In particular, distribution patterns were not consistent with an effect of terrestrial runoff. This study provides evidence of an exceptionally lethal effect on corals by a single species of filamentous alga, and emphasizes the species-specific nature of coral-algal competitive outcomes, even within a functional group.

KEY WORDS: Coral-algal competition · *Anotrichium tenue* · Epilithic algal community · Filamentous algal turfs · *Porites* spp.

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INTRODUCTION

Competition between corals and benthic algae is centrally important to the structure and condition of coral reefs. Recent controversy over the relative importance of top-down (Hughes 1994, Hughes et al. 1999, Aronson & Precht 2000) versus bottom-up (Lapointe 1997, 1999) factors in controlling macroalgal blooms during reef degradation has focused on the processes

that control algal abundance. However, both perspectives tend to assume competitive superiority of algae over corals, whereby an increase in algal abundance will lead to a decrease in abundance of corals (McCook 1999). Despite the importance of algal competition with corals, there have been very few studies critically examining the nature of coral-algal interactions (McCook et al. 2001), and particularly few that unequivocally demonstrate competition as the cause of

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observed changes (e.g. discussed by Underwood 1986, McArdle 1996). In many cases, algal overgrowth may be the consequence, rather than the cause, of coral mortality or damage (Diaz-Pulido & McCook 2002).

In a recent review (McCook et al. 2001), we suggested that available evidence indicates that coral-algal competition is widespread, but that the interaction is highly variable in both process and outcome, and should not be considered as simple or uniform. Several studies have shown negative effects of algae on corals (Hughes 1989, Coyer et al. 1993, Jompa & McCook 2002), reducing coral growth, fecundity and recruitment (Tanner 1995, Miller & Hay 1996, 1998). However, other studies have indicated slightly negative to neutral effects (Lirman 2001, McCook 2001) and one study even showed a positive effect, by reducing coral bleaching (Jompa & McCook 1998). The interaction is not one-sided, as corals may inhibit algal growth or even overgrow the algae (de Ruyter van Steveninck et al. 1988, van Woesik 1998, McCook 2001, Jompa & McCook 2002).

It appears that much of this variability can be understood in terms of the limited number of competitive mechanisms by which benthic algae can affect corals (McCook et al. 2001). Algal functional groups (Littler 1980, Steneck & Watling 1982, Littler & Littler 1984, Steneck & Dethier 1994), based on the ecological properties and physical structure of the algae, are able to provide an effective summary of the competitive potential of different algae, based on the potential for those mechanisms. For example, filamentous algal turfs and canopy-forming leathery macrophytes have very different potential to inhibit corals. Canopy-forming macrophytes may effectively shade large areas of substrate but, having relatively small holdfasts, will not directly overgrow or smother significant areas of live coral tissue (McCook et al. 2001).

However, even within a functional group, there may be considerable differences in competitive potential between algal taxa. For example, filamentous algae have been reported both to overgrow and kill corals (Potts 1977, Littler & Littler 1997), and to be overgrown and displaced by corals (McCook 2001), particularly during recovery from lesions (Bak et al. 1977, Meesters et al. 1994, van Woesik 1998). Early in 1999 we observed an unusually high number of massive *Porites* spp. colonies with patches of overgrowth by a single species of turfing, filamentous red alga (*Anotrichium tenue*) on the fringing reefs of the Palm Islands, Great Barrier Reef (GBR). This phenomenon provided an opportunity to compare the competitive effects of this species with that of the general, mixed-species filamentous turfs, thus allowing comparison within an algal functional group.

MATERIALS AND METHODS

Approach. This study describes the extent and process of *Anotrichium tenue* overgrowth and its effects on corals using a combination of several approaches. These comprised (1) a detailed description of the colonisation process at a small scale; (2) an experimental test to determine the extent to which *A. tenue* or mixed-species algal turfs were the direct cause of mortality of coral tissue; (3) broader-scale observations, intended to establish the extent to which the patterns described in the more detailed work were site- or species-specific. These observations include: a comparison of the time course of overgrowth at 2 reefs; surveys of the occurrence of *A. tenue* overgrowth at a cross-continental shelf scale; and surveys of the specificity of *A. tenue* infection to particular coral taxa.

Study sites. Most of the detailed monitoring work and the experimental study were conducted at 3 to 5 m depth on the reef slopes of the fringing reef at Cannon Bay, Great Palm Island, on the inshore central GBR (Fig. 1; 18° 41.1' S, 146° 35.2' E). This site is located approximately 30 km from the coast and has approximately 20% cover of massive *Porites* spp., predominantly *P. lobata*, *P. lutea* and *P. australiensis*. The time course of *Anotrichium tenue* 'infection' at this site was compared to that at a site at Pioneer Bay, Orpheus Island (18° 36.4' S, 146° 29.4' E) at approximately the same depth (3 to 5 m). The latter site was dominated also by massive *Porites* spp. and is situated about 20 km from the coast. The frequency of *A. tenue* overgrowth was surveyed at 7 reefs across the continental shelf in the central section of the GBR (Fig. 1). Surveyed reefs ranged from those very close to the mainland and strongly influenced by terrestrial runoff (Goold Island and Pandora Reef, approximately 12 km offshore), through inshore (Orpheus Island and Great Palm Island) and mid-shelf reefs (Rib and Trunk, approximately 60 km from the coast) to the outer shelf (Myrmidon Reef, approximately 110 km from the coast), where terrestrial influence is minimal (for more detailed descriptions of the study reefs see Done 1982, Russ & McCook 1999, McCook 2001).

Methods. *Anotrichium tenue* colonisation of live coral tissue—small-scale patterns: Description of *A. tenue* colonisation patterns involved monitoring changes in the area occupied by healthy, damaged and dead coral tissue, the area of *A. tenue* overgrowth, and the area of general, mixed-species algal turfs (Fig. 2A). *A. tenue* is usually pale pink or brown, the thallus sparsely branched, with most axes loosely prostrate (with erect axes of ~0.5 to 1 cm height) and attached to corallites by rhizoids (Fig. 2B). *A. tenue* overgrowth of massive *Porites* spp. usually occurred at the lower edge of the live coral tissue, forming distinct bands or

Fig. 1. Map of central GBR showing study sites ranging from innermost inshore (Goold Island and Pandora Reef) reefs through inshore (Orpheus Island and Great Palm Island) to mid-shelf (Rib and Trunk Reefs), and outer-shelf (Myrmidon Reef) reefs. In comparison to mid- and outer-shelf reefs, inshore reefs are affected by relatively high inputs of terrestrial sediments and nutrients, with Goold Island strongly influenced by sedimentation and flood plumes from Herbert River (lightly shaded; further details in McCook 2001)

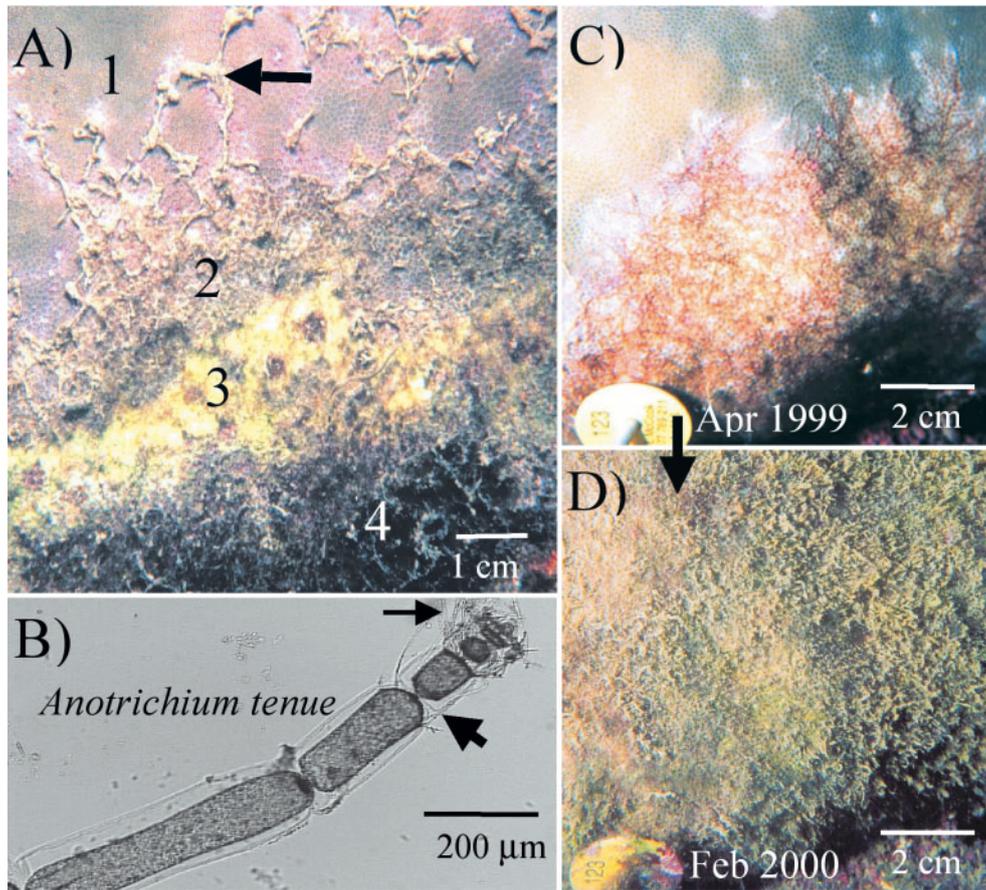
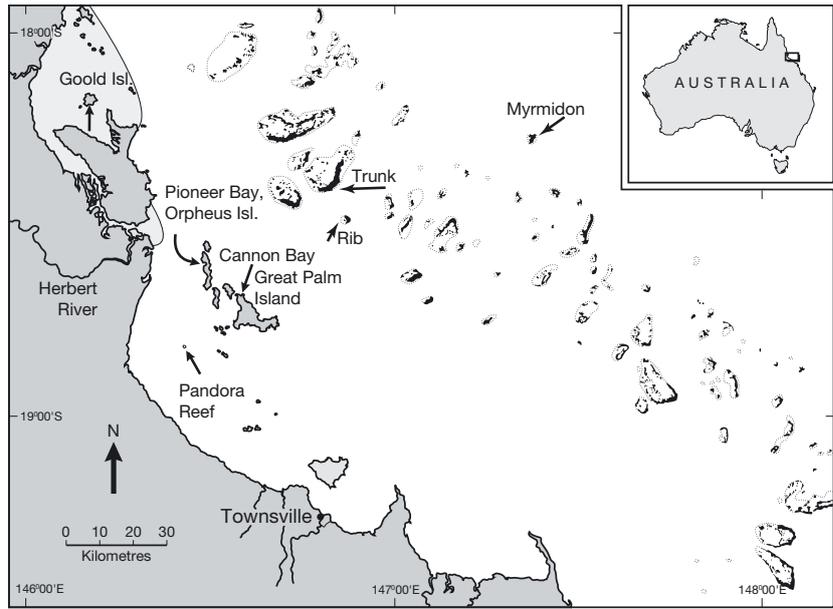


Fig. 2. *Anotrichium tenue*, a filamentous red alga, overgrowing the massive coral *Porites* spp. (A) Algal overgrowth forms 4 distinctive 'zones': (1) healthy coral tissue; (2) live coral colonised by *A. tenue*; (3) recently dead coral (bleached); (4) mixed algal turf. Observations of the time course, and experimental work, showed that the process involved active encroachment of *A. tenue* onto live coral tissue, causing coral death. Arrow shows single algal filaments trapping substantial quantities of sediment, apparently enhancing damage to underlying coral tissue. (B) Distinctive characteristics of an apical branch of *A. tenue* include transverse segmentation jointed with pit-connections (lower, thicker arrow) and trichoblasts around the apical cells (upper, thinner arrow). (C) Plot with *A. tenue* present in initial month, showing alga growing on live tissue of massive *Porites*, causing pale and bleached coral tissue, and encroaching toward healthy tissue. (D) Same plot (as in C) in final month, showing all coral tissue in plot overgrown by mixed algal turf

zones (Fig. 2A). Descriptions are based on photographic monitoring of fixed plots, qualitative observations of wider areas, and microscopic identification of samples of algal turfs from within the relevant zones.

Effects of *Anotrichium tenue* and mixed algal turfs on corals—experimental test: The second approach involved an experimental test to determine the extent to which *A. tenue* actually caused damage or death of coral tissue, rather than simply overgrowing coral tissue damaged by some other unknown cause, and to compare the effects of overgrowth by *A. tenue* and general mixed-species algal turfs. The experimental design compared mortality of coral tissue in 3 treatments: (1) plots in which *A. tenue* was naturally present; (2) plots in which *A. tenue* was originally present but had been experimentally removed; and (3) plots in which mixed algal turfs were naturally present and *A. tenue* was not. Thus, any difference in coral mortality between the first 2 treatments could be assumed to be due to *A. tenue* overgrowth, and the third treatment provided a comparison with the more widespread general mixed-species filamentous algal turfs, indicating the extent to which any effect was specific to *A. tenue*.

Each treatment included 10 replicate small ($10 \times 10 \text{ cm}^2$) plots located on massive *Porites* spp. colonies, chosen to include approximately 50% healthy coral tissue, and marked with nails and tags. We selected 20 plots to include *Anotrichium tenue* (e.g. Fig. 2C), 10 of which were randomly allocated to the *A. tenue* removal treatment and the rest left intact as controls (*A. tenue* present); 10 plots were also placed on the border between healthy coral tissue and mixed-turf algae overgrowing dead coral skeleton. Plots were generally on the lower side of the coral colony. The *A. tenue* removal treatment involved carefully removing the alga from the plots at the beginning of the experiment, either by hand or with a fine-pointed hobby knife, minimizing damage to underlying coral tissue. *A. tenue* did not generally recolonize the coral tissue following initial removal, so that subsequent algal removal was not necessary.

Plots were mapped in the field and monitored photographically at 5 dates over a period of 10 mo from April 1999 to February 2000. As *Anotrichium tenue* overgrowth generally formed 4 distinct zones (Fig. 2A), we estimated the area of (1) healthy coral tissue; (2) *A. tenue* growing on live coral tissue; (3) recently dead coral skeleton; and (4) mixed algal turfs. Areas were estimated from slides projected onto a 100 cm^2 grid representing the $10 \times 10 \text{ cm}^2$ plots, referring to field-drawn maps where necessary. Data analysis was based on the change in percent cover of dead coral within each plot relative to cover at the initial date (i.e. % cover of dead coral tissue at each date minus % cover

of dead tissue on initial monitoring date in April 1999; referred to as 'mortality of coral tissue'). Dead coral tissue included recently dead coral skeleton and established mixed algal turfs (Zones 3 and 4 in Fig. 2A). Data were tested for treatment effects on the final date, using a 1-way ANOVA with treatments as a fixed factor, and Student-Newman-Keuls test (SNK; at $p = 0.05$). We also tested the significance of the changes through time using a paired *t*-test to compare initial and final cover of dead coral tissue in each plot. Data were examined for homogeneity of variance (Cochran's test), independence and normality of residuals (graphically).

Distribution and species-specificity—larger-scale patterns: To place the detailed and experimental work in a broader context, we examined 3 aspects of *Anotrichium tenue* overgrowth: the time course of overgrowth, the occurrence and frequency of overgrowth across the continental shelf, and the specificity of the overgrowth to massive *Porites* spp. The time course of overgrowth and extent of mortality of coral tissue was compared over 10 mo at 2 reefs (Cannon Bay, Palm Island, and Pioneer Bay, Orpheus Island) separated by about 15 km. Ten plots with *A. tenue* present were established at Pioneer Bay, for comparison to the similar plots established at Cannon Bay. A Student's *t*-test was used to compare the mortality of coral tissue between the 2 sites after 10 mo (mortality calculated as detailed in preceding subsection).

Frequency of *Anotrichium tenue* overgrowth of live coral tissue was surveyed on 7 reefs across the continental shelf in the central section of the GBR (Fig. 1). Surveys involved 3 to 6 dives of approximately 1 h each around reef crests and slopes at all sites, recording frequency of occurrences and taxa of coral overgrown (numbers of massive *Porites* spp. colonies surveyed at each reef were at least 12 at Goold Island, 15 at Pandora Reef, 42 at Pioneer Bay, 40 at Cannon Bay, 25 at Rib Reef, 15 at Trunk Reef and 30 at Myrmidon; in total, approximately 107 patches of *A. tenue* were observed). Although *A. tenue* overgrowth is quite distinctive in appearance and easily distinguishable in the field (e.g. Fig. 2A,C), we collected samples of the alga for microscopic confirmation of the species identification.

RESULTS

Anotrichium tenue colonisation of live coral tissue—small-scale patterns

Observations and photo-monitoring showed that most live coral tissue overgrown by *Anotrichium tenue* eventually died. The time course of colonisation fol-

lowed a fairly uniform pattern: *A. tenue* colonised live coral tissue, generally, but not always, at the boundary between dead coral skeleton and mixed algal turfs (Fig. 2A: Zone 2). The colonised coral tissue bleached and then died. *A. tenue* filaments disappeared from the dead coral tissue (Fig. 2A: Zone 3), apparently colonising adjacent, live coral tissue. The dead coral tissue was subsequently colonised by blue-green algae and 1 to 2 mo later by mixed-species filamentous algal turfs (Fig. 2A: Zone 4). Microscopic examination of algal specimens indicated that the recently dead area (Zone 3) was generally dominated by thin blue-green algae, including *Schizotrix* spp., *Calothrix* spp., Oscillatoriales and Coccogonales. Composition of the mixed algal turfs became similar to those on the mixed algal turf treatment plots, and were generally dominated by species of *Polysiphonia*, *Cladophora*, *Centroceras*, *Sphacelaria*, *Hincksia*, *Ostreobium*, *Herposiphonia*, with very little, if any, *A. tenue*.

Coral tissue overgrown by *Anotrichium tenue* was generally bright pink in colour, apparently a symptom of stress caused by the presence of the alga. We often observed substantial amounts of sediments and mucus adhering to individual filaments of *A. tenue* (Fig. 2A: arrow). Removal of this sediment sometimes revealed pale, bleached or dead coral tissue underneath. It appears that this trapped material may increase or accelerate the extent of coral tissue damage.

Effects of *Anotrichium tenue* and mixed algal turfs on corals—experimental test

Mortality of coral tissue was markedly and significantly higher in plots with *Anotrichium tenue* present than in plots from which *A. tenue* had been experimentally removed (demonstrating that *A. tenue* was in fact the direct cause of much of the damage to coral tissue) or in plots with general mixed-species algal turfs present (demonstrating that the effect was specific to *A. tenue*: Fig. 3, final month; Table 1; SNK). Cover of dead coral tissue in the plots with *A. tenue* present increased significantly over the 11 mo of the experiment (paired *t*-test $p = 0.0006$). In contrast, mortality was much less in the plots with *A. tenue* removed ($p = 0.051$), and negligible in the plots with mixed species turfs ($p = 0.55$).

Thus, relative to the general, mixed-species algal turfs, *Anotrichium tenue* was exceptionally effective at overgrowing and killing the coral tissue. The mixed algal turfs were relatively harmless to the corals. The slight increase in coral mortality in the *A. tenue* removal treatment at the end of the experiment was apparently caused by new *A. tenue* colonisation in 2 plots.

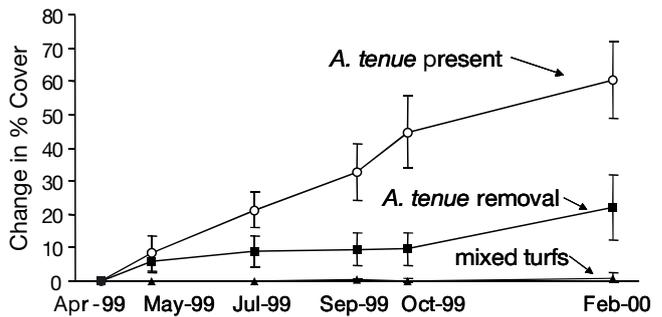


Fig. 3. *Porites* spp. Time course of mortality of coral tissue in each treatment at Cannon Bay, Great Palm Island. Data are changes in percent cover of dead coral tissue (Zones 3 and 4 in Fig. 2A) relative to initial monitoring month (i.e. final % dead tissue minus initial % dead tissue; means \pm SE, $n = 10$; because data are from 10×10 cm quadrats, a 1% change corresponds to death of 1 cm^2 coral tissue). Mortality of coral tissue was significantly higher in plots with *Anotrichium tenue* present than in the other treatments (Table 1; SNK test; *A. tenue* removal and mixed-turf treatments were not significantly different)

Distribution and species-specificity—larger-scale patterns

The overall time course of *Anotrichium tenue* overgrowth was very similar at Cannon Bay and Pioneer Bay (Fig. 4). Mortality of coral tissue at the end of the study was also similar for the 2 sites (*t*-test: $p = 0.7$). *A. tenue* showed a general, gradual decline at both sites over the 10 mo period of the study, indicating that *A. tenue* patches are ephemeral, and persist for approximately 1 yr.

Surveys of reef crests and slopes indicated that 60% of the massive *Porites* spp. colonies at Cannon Bay and 40% of those at Pioneer Bay had patches of *Anotrichium tenue* overgrowth, with patches varying between 50 and 200 cm in length and up to 5 cm in width. In contrast, the phenomenon was relatively scarce at Pandora Reef (~5% of colonies surveyed) and was not found at the very inshore reef (Goold) nor at the mid-shelf (Rib and Trunk) and outer-shelf (Myrmidon) reefs. The majority of corals observed with *A. tenue* overgrowing live tissue were massive *Porites* spp. (predominantly *P. lobata*, *lutea* and *australiensis*), although, much less frequently, the alga was also observed overgrowing live foliose *Turbinaria* spp., en-

Table 1. *Porites* spp. One-way analysis of variance of effects of treatment on mortality of coral tissue by final month (Fig. 3)

Source	df	MS	F	p
Treatment	2	9094	11.62	<0.001
Error	27	782		

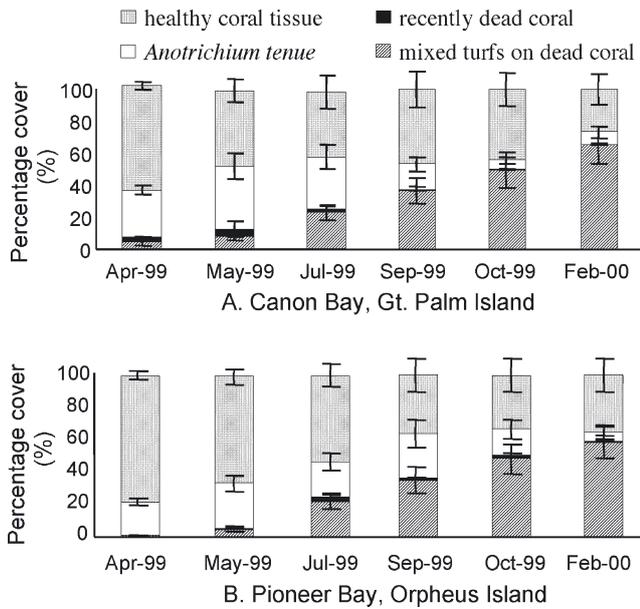


Fig. 4. *Anotrichium tenue* overgrowing *Porites* spp. Changes in percent cover for each zone (Fig. 2A) at Cannon Bay, Great Palm Island, and Pioneer Bay, Orpheus Island. Data are means (\pm SE, $n = 10$) for each zone

crusting to foliose *Montipora* spp. and branching *P. annae*. No other coral species were observed with *A. tenue* overgrowth, including the branching *P. cylindrica*, a widespread and abundant species in this area. Overgrowth appeared generally to develop at the border between the live coral and mixed algal turfs, although approximately 5% of *A. tenue* patches occurred completely within live coral tissue, suggesting that the alga was able to attach to live tissue either by settlement or by vegetative fragmentation. Massive *Porites* spp. colonies of up to 50 cm diameter were observed to have been completely killed, apparently by *A. tenue* overgrowth.

DISCUSSION

The combined small-scale observations and experimental results provide strong evidence that overgrowth by *Anotrichium tenue* is the direct cause of coral tissue death rather than simply a symptom or consequence of previous tissue damage or coral stress. Given the scarcity of experimental evidence for coral-algal competition (McCook et al. 2001), this study is significant simply as a clear demonstration of competitive overgrowth of live coral by a benthic alga.

However, this overgrowth also stands in strong contrast to the results for the general mixed-species algal turfs, which were not able to overgrow the live coral tissue in any of the plots. This suggests that these turfs

were very poor competitors with the corals. Previous experimental work in this area (McCook 2001) showed that the presence of these mixed-species turfs was having little inhibitory effect on the corals, whereas the corals were inhibiting the algal turfs. The interpretation here, that the competitive ability of *Anotrichium tenue* is exceptional among the filamentous turfing algae (Figs. 3 & 4), is strengthened by the observations that (1) the general turfs are a mixture of a large number of species, none of which overgrew live coral tissue, and (2) the *A. tenue* patches have much lower biomass (per unit area) than the mixed turfs, yet are still much more effective competitors. Mixed turf colonisation generally followed coral tissue death caused by *A. tenue*, so that *A. tenue* appears to act as a colonizing species, in effect creating new substrate but subsequently being replaced by more typical turfs.

Thus it seems that the ability of *Anotrichium tenue* to overgrow and kill live coral tissue is exceptional and that, in general, filamentous algal turfs are not able to overgrow live coral tissue but are relatively poor competitors, having little effect on corals (McCook et al. 2001). Only 2 previous published studies have reported lethal effects of algal turfs on corals. Potts (1977) suggested that mixed-turf algae caused coral mortality as a result of the metabolic costs to the corals of removing sediments trapped by the turf algal mats. Littler & Littler (1997) found that a non-filamentous but turf-forming macroalga *Dasyopsis spinuligera* overgrew corals in the Caribbean. They suggested that the likely mechanism involved was allelochemical or a secondary substance produced by the alga causing coral death. In contrast, most studies have reported minor effects of algal turfs on corals, or have even suggested that corals were competitively superior to the algal turfs (e.g. Fishelson 1973, Bak & Steward-van Es 1980, Meesters et al. 1994, van Woesik 1998, McCook 2001).

It is useful to consider the mechanisms that might allow *Anotrichium tenue* to exert such exceptional effects on the corals. Two factors seem relevant, the ability to colonize live coral tissue despite defensive mechanisms by the corals (such as stinging, mucus secretion, etc.; Lang & Chornesky 1990), and the ability to kill underlying coral tissue. Although we do not have direct evidence, it appears likely that both these abilities are facilitated by allelochemical substances produced by the alga, as the patterns of coral tissue death are not consistent with any of the other competitive mechanisms that enable algal overgrowth of corals (see Table 5 in McCook et al. 2001). Numerous other filamentous algae from the same family as *A. tenue* (the Ceramiaceae), with similar growth habits (i.e. creeping and branching, with erect axes and rhizoids; Price & Scott 1992) were abundant among the mixed-turf algae at

the study sites. However, only *A. tenue* was observed overgrowing massive *Porites* spp. corals. If the potency of *A. tenue* is chemically based, this would illustrate a limitation of the accepted functional groups of algae (Littler 1980, Steneck & Dethier 1994) in describing competitive properties of algae (as suggested by McCook et al. 2001). These groups are based primarily on physical properties of the algae (height, density, toughness, etc.), and hence are less effective at explaining ecological properties which are chemically mediated.

Our observations also suggest that the extent of damage to coral tissue was significantly increased by the tendency of individual *Anotrichium tenue* filaments to trap coral mucus and/or sediments and detritus (e.g. Fig. 2A: arrow). By interfering with the cleaning mechanisms of the coral, the alga may cause stress to areas of tissue much larger than otherwise overlain by the relatively small algal filaments.

It is intriguing that *Anotrichium tenue* overgrowth was relatively specific, so that whatever the mechanisms involved, they appear effective for relatively few taxa of corals. This specificity is difficult to interpret, since it is not obviously related to either growth form or taxonomic affinities. Although most common on massive *Porites* spp., and recorded on the branching *P. annae*, we never recorded *A. tenue* on the branching *P. cylindrica*, which is widespread, and particularly abundant at Cannon Bay and Pioneer Bay. In contrast, we frequently observed another filamentous Ceramiales, *Corallophila huysmansii*, overgrowing *P. cylindrica* on these reefs, but did not find it on massive *Porites* spp. (Jompa & McCook 2003, this volume). *P. cylindrica* has similar sized corallites (~1.5 mm) to the massive *Porites* species studied here. Similarly, our observations of *A. tenue* on foliose, encrusting and branching corals are not consistent with a specificity to a particular life-form.

The combined results of the broader surveys and the comparison of overgrowth between sites suggest that the phenomenon is not widespread, but that the effects are not site-specific: wherever *Anotrichium tenue* overgrowth occurs, it is likely to have similar effects to those documented here. Although *A. tenue* was more abundant on live corals at Cannon Bay than at Pioneer Bay, the pattern of coral overgrowth was similar at both sites. A survey of algal turf settlement on inshore reefs in this area (authors' unpubl. data) indicated that *A. tenue* is not common in algal turfs, and was more common on Great Palm Island than on other islands in the Palm group, or on Goold Island. The species has also been reported from Malaysia (Masuda et al. 1999) and South Africa (Norris & Aken 1985), and so is presumably widespread. Thus, although the results do not suggest that this alga poses a significant threat, as a pathogen, to coral populations at larger spatial scales,

it is possible that the overgrowth phenomenon is quite widespread. *A. tenue* overgrowth was not recorded on either the reef most influenced by terrestrial runoff, nor the reefs most removed from such influences, suggesting that the phenomenon is unlikely to be related to anthropogenic changes in terrestrial runoff.

In summary, the results of this study demonstrate a marked contrast in competitive effects on corals between a single species of turfing, filamentous red alga, *Anotrichium tenue*, and a broad range of species with similar growth forms and even taxonomic affinities. The other species present in the general algal turfs at these sites were not able to colonize or significantly affect live tissue of massive *Porites* spp. colonies, whereas *A. tenue* was able to colonize live coral tissue, causing tissue death and serving as a colonizing species for general algal turfs. It appears that this competitive ability may be due to allelochemical or similar properties, but is limited to a relatively few coral taxa. The results illustrate the extent of variability in the processes and outcomes of coral-algal interactions, even within an algal functional group, algal family, and coral life-forms and genera. Although coral-algal competition may be widespread on coral reefs, the outcomes will vary considerably, and cannot be considered as a simple, uniform process.

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